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Can we save large carnivores without losing large carnivore science?

Running title: Saving large carnivore science

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Abstract

Large carnivores are depicted to shape entire ecosystems through top-down processes. Studies describing these processes are often used to support interventionist wildlife management practices, including carnivore reintroduction or lethal control programs. Unfortunately, there is an increasing tendency to ignore, disregard or devalue fundamental principles of the scientific method when communicating the reliability of current evidence for the ecological roles that large carnivores may play, eroding public confidence in large carnivore science and scientists. Here, we discuss six interrelated issues that currently undermine the reliability of the available literature on the ecological roles of large carnivores: (1) the overall paucity of available data, (2) reliability of carnivore population sampling techniques, (3) general disregard for alternative hypotheses to top-down forcing, (4) lack of applied science studies, (5) frequent use of logical fallacies, and (6) generalisation of results

from relatively pristine systems to those substantially altered by humans. We first describe how widespread these issues are, and given this, show, for example, that evidence for the roles of wolves (*Canis lupus*) and dingoes (*Canis lupus dingo*) in initiating trophic cascades is not as strong as is often claimed. Managers and policy makers should exercise caution when relying on this literature to inform wildlife management decisions. We emphasise the value of manipulative experiments, and discuss the role of scientific knowledge in the decision-making process. We hope that the issues we raise here prompt deeper consideration of actual evidence, leading towards an improvement in both the rigour and communication of large carnivore science.

Keywords: apex predator; behaviourally-mediated trophic cascades; adaptive management; experimental design; mesopredator release hypothesis; science denial

Introduction

Large carnivores are some of the most charismatic and ecologically-influential organisms on Earth. Through their interactions with other animals, large carnivores may affect faunal and floral communities across multiple trophic levels ([Darwin 1859](#); [Leopold 1949](#); [Hairston *et al.* 1960](#)). This process is known as a trophic cascade ([Paine 1980](#)), and is a concept now fully entrenched amongst ecologists, conservation biologists and many land and wildlife managers.

Seldom have such novel ecological concepts been so rapidly mainstreamed to the extent that they are identified as one of the 20 most influential topics in biodiversity conservation ([Bradshaw *et al.* 2011](#)). Yet the ‘mesopredator release hypothesis’ (MRH) and its cousins the ‘large-carnivore control-induced trophic cascade hypothesis’ (TCH) and the ‘behaviourally-mediated trophic cascade hypothesis’ (BMTCH) have done exactly that, so much so that these concepts are now routinely advanced as scientific and moral justification for what are essentially highly normative standpoints concerning desired conservation outcomes. Inherently value-laden, religious terms are now frequently used in academic discourses about the ecological roles of large carnivores – terms such as hero, doctrine, dogma, demonising, virtuous, saviour, scapegoat, sanctification, sinners and saints (e.g. [Jones 2002](#); [Soulé *et al.* 2005](#); [Anahita and Mix 2006](#); [Allen *et al.* 2011a](#); [Letnic *et al.* 2011](#); [Mech 2012](#); [Chapron and Lopez-Bao 2014](#); [Middleton 2014](#); [Johnson and Wallach 2016](#)). Unfortunately, but perhaps

motivated by the dire status of many carnivore populations, a growing number of studies rely on weak inference to assess the roles of large carnivores in ecosystems (e.g. [Allen et al. 2013b](#); [Ford and Goheen 2015](#)). Such practices might stimulate short-term gains in carnivore conservation and motivate some segments of the public to care about it, but these communication practices risk undermining long-term confidence in large carnivore science and scientists ([Fleming et al. 2012](#); [Sarewitz 2012](#); [Middleton 2014](#)). The actual *science* of large carnivore science is getting lost, being replaced by catch phrases, slogans, sound bites, YouTube clips, fake news and post-truth politics, or the simplification and popularisation of unsubstantiated or unreliable theories and hypotheses. This tension between scientific rigour and pursuit of quick conservation gain raises the critical question: can ecologists save large carnivores without losing large carnivore science?

As described in several studies (summarised, for example, in [Crooks and Soulé 1999](#); [Hayward and Somers 2009](#); [Terborgh and Estes 2010](#); [Eisenberg 2011](#); [Estes et al. 2011](#); [Ritchie et al. 2012](#); [Ripple et al. 2014b](#); but for a clear definition see [Ripple et al. 2016b](#)), the core theoretical processes associated with the MRH, TCH and BMTCH are:

1. Mesopredators and herbivores induce declines in smaller fauna and flora,
2. Large carnivores induce declines in mesopredators and herbivores,
3. Lethal control, harvest or hunting of large carnivores by humans induces declines in large carnivores, increases in mesopredators and herbivores, and ultimately causes undesirable outcomes for biodiversity and ecosystems,
4. Cessation of large carnivore control, harvest or hunting and/or active large carnivore encouragement, including reintroduction, induces declines in mesopredators and herbivores, which ultimately causes desirable outcomes for biodiversity and ecosystems, and
5. Documentation of the MRH, TCH and BMTCH in some studies has been common enough that these processes should be considered universal across ecosystem types and independent of carnivore size or phylogeny.

The way these theories have been mainstreamed are perhaps best encapsulated in the short online video titled *How wolves change rivers* ([Sustainable Human 2014](#)), which has been

viewed over 18 million times since early 2014, but which does not consider the contrary (and often superior) evidence for the processes it claims. Proponents of the MRH, TCH, and BMTCH argue that these hypotheses should be accepted by scientists and society as ecological laws by default (not as mere theories or hypotheses) and that the burden of proof for demonstrating their reality should be placed on those who do not believe them ([Estes et al. 2011](#)). These theories also provide the scientific justification for many admirable and worthwhile efforts to restore large carnivore populations to densities and distributions reminiscent of former times ([Ripple et al. 2014b](#); [Ripple et al. 2016a](#)), although historical ecological benchmarks have not been determined for most systems (e.g. [Hayward 2012](#)). Nevertheless, the worldwide influence of the MRH, TCH and BMTCH have been enormous ([Bradshaw et al. 2011](#)). In spite of the perceived universality of top-down control of ecosystems however, there is a large and growing number of large carnivore studies indicating that such effects are highly context specific and that many of the most rigorous studies failed to document evidence of trophic cascades (Tables 1–3).

INSERT TABLE 1

INSERT TABLE 2

INSERT TABLE 3

In this brief overview, we summarise six key issues weakening the strength of the available literature and undermining scientific advancement on understanding large carnivores' ecological roles. We focus our discussion on grey wolves (*Canis lupus*) and Australian dingoes (*Canis lupus dingo*), which have been claimed to be the only two terrestrial carnivores for which both the MRH and TCH have been demonstrated (Figure S2 in [Ripple et al. 2014b](#)). Our aim is not to denigrate these or other large carnivores, decrease interest in them, diminish the motivation to conserve them, or hinder the pursuit of scientific knowledge in this field. On the contrary, our aim is to outline the primary issues weakening the reliability of research on MRH, TCH and BMTCH, to show why wildlife managers and policy makers should exercise caution when making decisions based on the currently available literature describing these processes. We agree with many authors that top-down forcing can occur and that large carnivores can have important ecological roles. However, there are enormous gaps in our understanding of when and where such effects will occur in most systems. Articulating the truth about the reliability (or lack thereof) of large carnivore science is, in and of itself, a

strong conservation message: it is far better to err on the side of caution and preserve large carnivores in the first place than to falsely believe ecosystems can be quickly and easily fixed, restored or rewilded by simply bringing some carnivores back ([Glen et al. 2007](#); [Marshall et al. 2016](#)). We further offer suggestions for overcoming these issues with the hope that future large carnivore studies will avoid them and better contribute to the evidence-base needed for the management and conservation of large carnivores and sympatric species.

Issues that weaken the available literature supporting the MRH, TCH and BMTCH

1. There is not enough evidence of any kind, reliable or otherwise

A general understanding of large carnivores' roles is only beginning to emerge, and much more work is needed before we can confidently claim what those roles are or the ecological contexts that shape these roles. Large carnivores unquestionably have ecological effects or impacts of some description. In principle, every individual animal eaten by a carnivore represents an impact – the prey animal is dead or scared, the prey's population growth or foraging is slowed, scavengers scavenge, decomposers decompose, nutrients enter the soil, life for the prey's competitor is now a little easier, the vegetation that would have been consumed by the prey survives a little longer, and the carnivore lives to kill another day. Whether the death of that prey animal is a good or bad thing (or not) depends on the perspective of which animal is favoured over another ([Allen et al. 2011b](#); [Mech 2012](#)) – there are winners and losers to every interaction ([Flagel et al. 2016](#)). These interactions all have a value, contributing to the building blocks of wider ecological and demographic processes, and evolutionary selection pressures ([Darwin 1859](#); [Hairston et al. 1960](#); [Kershaw 1969](#); [Barbosa and Castellanos 2005](#); [Krebs 2008](#); [Molles 2012](#)). But do these individual-level impacts of a relatively small magnitude combine and accumulate to produce detectable cascading impacts of a large magnitude on populations and whole ecosystems? Are these carnivore effects stronger or more important at shaping systems than bottom-up processes? Can individual carnivores regulate entire food webs? Do carnivore effects always produce net benefits to biodiversity? Are positive carnivore effects universal across ecosystems and apparent across all trophic levels?

In spite of claims for the universality of trophic cascades and a concomitant shift in the burden of proof to disprove top-down forcing and prove bottom-up forcing ([Terborgh and Estes 2010](#); [Estes et al. 2011](#)), Haswell et al. ([2017](#)) shows that at best, detectably large

cascading effects of top-predators (from a wide range of taxonomic groups) are the exception and not the rule. Indeed, several studies using strongly-inferential methods demonstrate that such top-down effects do not always occur, or if they do, they are far weaker than bottom-up processes (e.g. [Gasaway et al. 1983](#); [Boertje et al. 1996](#); [Hayes et al. 2003](#); [Vucetich and Peterson 2004](#); [Vucetich et al. 2005](#); [Brodie and Giordano 2013](#); [Marshall et al. 2013](#); [Allen et al. 2014b](#); [Ford et al. 2015a](#); [Sivy 2015](#); see also [Schmitz et al. 2000](#); [Bowyer et al. 2005](#); [Sergio et al. 2008](#); [McCoy et al. 2012](#); [White 2013](#); [McPeck 2014](#); [Kuijper et al. In press](#)). Ford and Goheen ([2015](#)) showed that of five strongly-inferential experiments investigating large carnivores' roles, only two found evidence supporting the TCH. Morgan et al. ([2017](#)) highlight the supremacy of bottom-up processes and articulate the folly of attempting to shoe-horn or apply outcomes from one ecological context into another. Recent global reviews of the topic have also reported that 'little is known' about 24 of the 31 species of the world's largest carnivores, as ecologists are only just beginning to discover their ecological functions ([Ripple et al. 2014b](#)); or put another way, the MRH, TCH and BMTCH have not yet been shown for at least 77% of large carnivores. Hence, we do not yet know what the ecological functions of large carnivores are, and what we do know is from a minority of species in an even smaller minority of biomes. While these hypotheses might eventually be applied to, and supported in, a wide number of food webs, evidence supporting these hypotheses are currently quite restricted.

Ripple et al. ([2014b](#)) claim that both the MRH and the TCH have been demonstrated only for two related species, grey wolves and Australian dingoes, but the evidence-base for these two species is very limited. In the case of dingoes, the total number of field studies on their ecological roles is just a few dozen. Of these studies, all but four are observational or correlative studies conducted in small areas (i.e. a few hundred km²) and over only a few days ([Allen et al. 2013b](#); [Allen et al. 2015](#)). Drawing on this limited pool of empirical data, the 22 literature reviews of dingoes' ecological roles produced over the last 10 years have unavoidably borrowed heavily from each other in what might be called citation inbreeding ([Allen et al. 2014c](#)). Thus, there is not a growing body of reliable evidence for dingoes' ecological roles at all, but merely a growing body of largely recycled literature (Table 1; see also [Allen et al. 2011b](#)). Evidence for the ecological roles of wolves is much stronger than dingoes, but is still frequently challenged and often found unreliable for similar reasons (Tables 2 and 3; see also [Winnie and Creel 2017](#)). The combination of mixed-outcomes when testing the MRH, TCH and BMTCH and the absence of studies on most species of large

carnivore warrants far greater circumspection than is often afforded in syntheses of carnivore ecology and conservation.

2. Sampling methods for carnivores are often unreliable

Studies measuring the effects of large carnivores roles typically correlate some change or difference within an ecosystem to some change or difference in carnivore abundance ([Ford and Goheen 2015](#)). But such approaches are frequently challenged because of their lack of rigour (Tables 1–3). These challenges usually fall into three main categories of complaint: experimental design constraints (e.g. manipulative experiments vs correlations or observations; alternative hypotheses), predator sampling strategies (e.g. tracking plots, camera traps, direct observations, movement data etc.), and data analysis approaches (e.g. indices, occupancy modelling, statistical assumption violations, exclusion/inclusion of outliers or contradictory data etc.). Counting or indexing carnivore populations can be difficult and is often associated with large confidence intervals, but analytical methods do exist to detect broad differences (e.g. [Kershaw 1969](#); [Caughley 1980](#); [Underwood 1997](#); [Zar 1999](#); [Quinn and Keough 2002](#); [Krebs 2008](#); [Engeman *et al.* 2017](#)). Unfortunately, many studies use carnivore sampling methods that are incapable of yielding reliable data on carnivore abundance, let alone actual rates of predation or perception of risk by prey animals. The absence of these data undermines evidence for the proposed link between variation in carnivore abundance and other reported changes and/or differences in the ecosystem.

Studies concluding that dingoes trigger trophic cascades are derived from non-validated and often confounded comparisons of population indices between habitats, season, and/or species ([Allen *et al.* 2011a](#); [Allen 2012b](#)). Ways to validate some common sampling methods have been developed ([Allen and Engeman 2014](#)). When their methods are scrutinised, the results of the most oft-cited works are unreliable ([Allen *et al.* 2014c](#)). Even the results of the best available manipulative experiments are sometimes contested on grounds that the predator sampling methods are unreliable (e.g. Table 1).

There is unlikely to ever be any one perfect predator sampling method that suits all applications, so the use of different sampling techniques and analytical methods across studies is not particularly concerning. It does not matter if carnivores are sampled using sand plots, camera traps, snow tracking, GPS collaring, direct observations, or remote sensing (for example) provided the data are subsequently handled and analysed appropriately. We argue

instead, that it is important to ensure that that whatever the implicit assumptions of the methods are, that they are justifiable for the context under which the study was conducted ([Engeman 2005](#); [Allen and Engeman 2014](#)). The weaknesses and limitations of these survey methods need to be openly acknowledged and discussed – not only in the peer-reviewed manuscript, but also in the subsequent public discourse. This is where many previous studies have erred (Table 1), and where improvements must be made if science is to acquire less ambiguous evidence to support the MRH, TCH or BMTCH ([Hayward et al. 2015](#)).

3. *Alternative hypotheses are seldom tested*

Carnivores are just one of many potential causal agents operating in ecosystems ([Vucetich et al. 2005](#); [Middleton 2014](#); [Peterson et al. 2014](#); [Ford and Goheen 2015](#)). Yet for many studies claiming support for the MRH, TCH and BMTCH, the study framework is designed to *create* evidence for these hypotheses rather than being designed so that evidence for plausible alternative hypotheses is both tested and compared at the same time ([Winnie 2014](#)). Studies investigating these hypotheses commonly focus on competition, predation/removal or risk of predation (Tables 1–3). But there are many more interaction types besides these within food webs, which interaction types can also be strong and often do not conform to simple expectations ([Muhly et al. 2013](#); [Saggiomo et al. 2017](#)). Invertebrate ([Meadows et al. 2017](#)) and theoretical (e.g. [Finke and Denno 2004](#); [Holt and Huxel 2007](#); [McCoy et al. 2012](#); [McPeck 2014](#); [Kendall 2015](#)) studies highlight many different outcomes of predator removal or addition, most of which have received little attention in the wider large carnivore literature ([Fleming et al. 2012](#); [Mech 2012](#); [Ford and Goheen 2015](#); [Haswell et al. 2017](#)). The consequence of not investigating plausible alternative explanations is that management actions may completely overlook key processes contributing to declines of fauna (e.g. [Allen 2011](#); [Middleton et al. 2013b](#); [Cooke and Soriguer 2017](#)), and they cannot discover these processes because the study framework simply corroborates a narrow set of *a priori* hypotheses without looking for others.

A clear example of the systemic failure to evaluate alternative hypotheses and ignore contrary data comes from a series of studies conducted in the Greater Yellowstone Ecosystem, USA ([Winnie 2014](#)). Environmental changes following the restoration of wolves to Yellowstone National Park are often given as a clear example of the beneficial effects of restoring large carnivores to ecosystems (Table 2), but there are alternative hypotheses to explain many of the observed changes ([Vucetich et al. 2005](#); [Marshall et al. 2013](#); [Middleton et al. 2013b](#)).

There is strong evidence that wolves alone are not responsible for all the changes attributed to them ([Mech 2012](#); [Winnie and Creel 2017](#)). Many other important changes to the Yellowstone system occurred around the same time as wolf restoration, and ‘when we tell the wolf story, we get the Yellowstone story wrong’ ([Middleton 2014](#)). Using data from 1961 to 2004, Vucetich et al. ([2005](#)) investigated the TCH and showed that changes in climate and harvest rate are justified explanations for most of the observed decline in Yellowstone elk, rather than heightened predation by wolves. Indeed, wolf predation was determined to be compensatory to existing rates of mortality (e.g. from starvation or mortality from other predators). In addition, early studies on the BMTCH reported that wolves scared herbivores away from riparian areas, which reduced herbivory on trees and ultimately caused increased tree growth ([Ripple and Beschta 2004](#); [Beschta and Ripple 2007](#)). Not only did these earlier studies incorrectly identify areas of high predation risk ([Creel et al. 2005](#); [Kauffman et al. 2007](#); [Kauffman et al. 2010](#); [Winnie 2012](#)), but they also failed to consider more parsimonious explanations for increased tree growth in riparian areas, such as the height of the local water table ([Bilyeu et al. 2008](#); [Kauffman et al. 2013](#)). MacNulty et al. ([2016](#); pg. 27) summarise the present situation when they state that ‘scientific consensus about the role of wolves in driving [trophic cascades] has yet to emerge, despite 20 years of research by numerous federal, state and academic investigators’, and that the ‘overarching reason for the impasse’ is the experimental design constraints on the Yellowstone wolf reintroduction program. In other words, the lack of rigour and strong inference in testing the MRH, TCH and BMTCH has generated the controversy over the role of wolves in restoring this Yellowstone landscape.

In Australia, snap-shot studies comparing fauna abundances in adjacent areas separated by predator-proof fences are commonly used to highlight the greater amount of biodiversity present on the side of the fence with a greater number of dingoes (e.g. [Letnic et al. 2009](#); [Fillios et al. 2010](#); [Letnic and Koch 2010](#); [Brawata and Neeman 2011](#); [Gordon et al. 2017a](#)). However, the relative abundances of dingoes is not the only important difference between the two sides of these fences (e.g. [Newsome et al. 2001](#); [Fitzsimmons 2007](#); [Allen 2011](#)). A range of important geological and biophysical differences are also present, not the least of which are the markedly different herbivore types, densities, and land-use histories, which are also well-known to structure fauna communities through grazing-induced habitat changes independent of dingoes or other predators ([Tiver and Andrew 1997](#); [Williams and Price 2010](#); [Parsons et al. 2012](#); [Howland et al. 2014](#); [Koerner and Collins 2014](#)). The cross-fence

differences are obvious, but their causes are not. In spite of the appearance of a grandiose ‘natural experiment’, the cross-fence comparisons are often poorly replicated and confounded. Nonetheless, studies adopting this design have formed the bulwark of claims about dingoes’ ecological roles ([Letnic et al. 2012](#); [Allen et al. 2013b](#); [Glen and Woodman 2013](#)). Until more rigorous experimental designs are implemented, further studies predicated on correlative, cross-fence differences does little to increase evidence for the ecological role of dingoes.

The management consequences of failing to address alternative hypotheses are exemplified by the relatively simple carnivore system in Australia. Johnson and colleagues ([2007](#)) argued that human control of dingoes in the last 200 years caused the continental collapse of marsupial communities across Australia, but the role of the continental invasion of European rabbits (*Oryctolagus cuniculus*; [Cooke and Soriguer 2017](#)) and the historical grazing of introduced sheep (*Ovis aries*) coupled with drought ([Allen 2011](#)) were not properly assessed as potential causal factors for marsupial decline. Johnson and colleagues continue to assert that if only dingo persecution stopped, dingoes would suppress introduced rabbits, red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*), and facilitate the recovery of reintroduced marsupials and other small mammals across the continent (e.g. [Johnson 2006](#); [Wallach et al. 2009](#); [Ritchie et al. 2012](#); [Letnic et al. 2013](#)). But such reintroductions continue to fail largely because predators – including dingoes – keep quickly decimating reintroduced mammals ([Christensen and Burrows 1995](#); [Moseby et al. 2011](#); [Bannister 2014](#); [Armstrong et al. 2015](#); [Bannister et al. 2016](#)). All the dingoes occupying Australia did not prevent the historical establishment and expansion of rabbits, foxes or cats across the continent in the first place, nor did the presence of dingoes prevent the collapse of marsupial communities following the advent of these pests. Extant dingo populations, never managed by modern humans across roughly one-third of the Australian continent ([Allen et al. 2015](#)), have not facilitated extirpation of these pests or their impacts, nor facilitated the recovery of marsupials in these areas. Indeed, dingoes reach their highest densities in places with abundant rabbits ([Bird 1994](#); [Allen 2012a](#)), suggesting that invasive species are supporting carnivores rather than large carnivores suppressing invasive species. Dingoes may even provide net benefits to invasive rabbits through mesopredator suppression, just as dingoes putatively benefit rabbit-sized native mammals ([Cooke and Soriguer 2017](#); [Gordon et al. 2017a](#)). In concert with habitat changes (be these caused by livestock, fire or rabbits), dingo predation has been identified as a key driver of native mammal decline independent of foxes or cats (e.g. [Kerle et](#)

[al. 1992](#); [Corbett 2001](#); [Lundie-Jenkins and Lowry 2005](#); [Barnes et al. 2008](#); [Allen 2011](#); [Allen and Fleming 2012](#); [Allen and Leung 2012](#)). Yet dingoes are typically considered part of the solution to Australia's fauna extinction crisis, when they are also part of the problem. Continuing to ignore this and other alternative hypotheses wastes precious time in our collective efforts to conserve native fauna under real threat of extinction.

In complex carnivore communities (where a wide variety of individual large carnivores utilise a range of hunting strategies, resulting in increased heterogeneity in predator-prey interactions), even manipulative experiments still struggle to tease apart the relative influence of top-down and bottom-up processes (e.g. [Gasaway et al. 1983](#); [Boertje et al. 1996](#); [Maron and Pearson 2011](#); [Sinclair et al. 2013](#); [Ford et al. 2015b](#); [Riginos 2015](#)). In fact, Riginos (2015) goes as far as to suggest that behaviourally-mediated trophic cascades are either weak or non-existent in African savanna systems because of the large sizes of many of the herbivores (elephants, *Loxodonta africana*, in particular) and the over-riding effect of climate. Predator diversity is known to dampen trophic cascade effects in model systems ([Finke and Denno 2004](#)), and top-down forcing is also known to attenuate down through trophic levels more rapidly than previously thought ([Schmitz et al. 2000](#); [Brodie et al. 2014](#)).

One characteristic of overemphasising the current robustness of large carnivore science is ignoring, suppressing or omitting reference to alternative hypotheses and contrary data ([Claridge 2013](#); [Winnie 2014](#)). This is easy for authors to do given the vast pool of citations to choose from (e.g. Tables 1–3) and the limited number of references a journal will typically accept. When accused of selective referencing, the plea of 'not enough room' (e.g. see [Marris 2014](#) for examples) does not promote objectivity and transparency. Rather, it disregards the legitimate scientific criticisms available and only widens the creeping cracks of bias described by Sarewitz (2012), who argued that research is riddled with systematic errors (see also [Ioannidis 2005, 2014](#)) and that the ensuing debate then erodes public confidence in science itself (see also [Fleming et al. 2012](#); [Middleton 2014](#)). Although large-scale and observational 'natural experiments' have great value when their results are 'consistent with' or 'inconsistent with' a given hypothesis, plausible alternative explanations nonetheless require thorough exploration and ranking before reported results from 'natural experiments' become the basis for changes in practice or policy ([Barley and Meeuwig 2016](#)). Investigating alternative hypotheses should be a greater priority in future research on large carnivore ecology.

4. *There is a dearth of applied-science studies*

Some research questions are largely academic (e.g. do species A and B have overlapping diets?), whereas applied studies have direct and immediate relevance to land and fauna managers (e.g. do interventions X and Y produce the same outcome for species A and B?). The importance of understanding the ecological roles of large carnivores has implications for the conservation and management of threatened carnivores and other fauna, such as livestock, game, or threatened wildlife prey species (e.g. [Boertje et al. 2010](#)). Managers need information that considers both the pros and cons of various management interventions, and this is best achieved through manipulative experiments or adaptive-management studies that investigate applied-science issues ([Glen et al. 2007](#); [Hone 2007](#); [Hone et al. 2015](#)). Questions about the conservation utility of large carnivores as tools to restore biodiversity across the landscape are answered much faster when truly applied questions are investigated.

Evidence for the effects of carnivore removal is also not the same thing as evidence for the effects of their recovery (e.g. anisotropic vs isotropic effects; *sensu* [Ford and Goheen 2015](#)). Simply re-establishing or bolstering large carnivores may not fix the many environmental problems that occurred as a result of (and/or in addition to) carnivore extirpation ([Marshall et al. 2013](#); [Marshall et al. 2014](#); [Wikenros et al. 2015](#)). In some cases, food web structure and ecological context may have changed irreversibly (for whatever reason), some niches may no longer exist, and a carnivore's function in the new ecosystem might now be different from their previous function. Changes in the physical environment caused by the removal of large carnivores may make the system resistant to complete restoration after large carnivores are restored. This 'change resistant' hypothesis was tested against the existing TCH in a replicated, randomized, manipulative experiment conducted over a decade. The hypothesis that wolf restoration had caused ecosystem reorganization was rejected ([Marshall et al. 2014](#)), yet subsequent literature ignored it and instead repeated the story (i.e. [Sustainable Human 2014](#)) that the ecosystems of Yellowstone have been dramatically restored by wolves following their reintroduction. Restoring carnivore populations "to areas greatly modified by human disturbance may not restore systems to their former state" ([Glen et al. 2007](#); pg. 498) and these new carnivore functions may not be viewed as desirable or produce net benefits to novel and still-changing ecosystems ([Fleming et al. 2012](#); [Flagel et al. 2016](#)).

Large carnivore studies often report a negative relationship between larger carnivores and smaller or mesocarnivores, and are then quick to recommend wholesale changes to the way large carnivores are managed without first measuring any actual effect of carnivore management (e.g. hunting, removal, restoration) on large or small carnivores, herbivores or prey (for examples, see [Letnic et al. 2009](#); [Wallach et al. 2010](#); [Colman et al. 2014](#); [Gordon et al. 2017a](#); [Gordon et al. 2017b](#)). Equally, perceived negative impacts of carnivores on livestock have historically been addressed by wholesale lethal control without any recognition of the positive impacts that carnivores may have on the herbivores that compete with livestock or the consequences of lethal control on livestock losses (e.g. [Wicks and Allen 2012](#); [Allen 2014](#); [Allen 2015a](#); [Prowse et al. 2015](#); [Allen 2017](#)). Treves et al. (2016) and others (e.g. [Reddiex and Forsyth 2006](#); [Doherty and Ritchie 2017](#)) rightly point out that many studies promoting predator control are badly designed, and we agree, but the same failing exists in many studies condemning predator control and promoting predator conservation. Unreliable science and poor science communication practices are a feature of literature expressing both positive and negative views towards carnivores ([Boertje et al. 2010](#)).

To make ecological data useful for improving carnivore management and conservation, researchers must provide managers with data they can apply. For example, when claiming that large carnivore control (i.e. trapping, hunting, or poisoning) must be banned in order to generate cascading, positive effects on biodiversity (e.g. [Carwardine et al. 2012](#)), information on the actual effects of carnivore hunting or poisoning on biodiversity are needed, not just information on how one carnivore species might interact with another (for examples, see [Fleming et al. 2012](#); [Allen et al. 2015](#)). Conversely, when claiming that large carnivore control must be implemented to reduce livestock predation, information on actual carnivore impacts and impact reduction is required to ethically justify carnivore control ([Braysher 1993](#); [Allen et al. 2014b](#); [Allen 2017](#)). The paucity of applied ecological data in the wider large carnivore literature means that much of the presently available information on the MRH, TCH and BMTCH is not as useful to managers as it could be. This paucity also means that, in most cases, we do not yet have a solid understanding of the actual cascading effects, if any, of carnivore reintroduction, population control or manipulation ([Ripple et al. 2014b](#); [Newsome et al. 2015](#)). This issue contributes to a significant knowledge-mobilization and implementation gap for large carnivore science.

5. Logical fallacies underpin much of the literature

Most research about the ecological roles of large carnivores is also grounded in two logical fallacies, *post hoc ergo propter hoc* and *cum hoc ergo propter hoc*. *Post hoc ergo propter hoc* is the notion that if X occurred before Y, then X caused Y. When X is undesirable, this pattern is often extended in reverse as: avoiding X will prevent Y. *Cum hoc ergo propter hoc* is the notion that if X changed similarly to Y, then X and Y are linked. The fallacies lie in coming to a conclusion based on the order or pattern of events, rather than accounting for other factors that might rule out a proposed connection.

Examples of *post hoc ergo propter hoc* in the large carnivore literature are rife and include, for example, conclusions to the effect that ‘the ecological changes observed in Yellowstone National Park occurred after wolves were reintroduced, so wolves must have caused these ecological changes’ (epitomised in [Sustainable Human 2014](#); see Table 2). Or alternatively, ‘the last population of highly endangered mammals went extinct after predator control, so predator control must have caused the extinction through trophic cascade effects’ (discussed in [Fleming et al. 2013](#)). There are also many examples of *cum hoc ergo propter hoc*, including almost all the relevant literature on dingoes’ ecological roles (see [Allen et al. 2013b](#); see Table 1). That wolves may not have been the cause of all the observed ecological changes in Yellowstone since the mid-1990s is argued by Kauffman et al. (2010), Mech (2012) and others (e.g. [Creel and Christianson 2009](#); [Winnie 2012](#); [Marshall et al. 2013](#); [Marshall et al. 2014](#); [Middleton 2014](#); [Peterson et al. 2014](#); see Table 2). The long term study of wolf–moose (*Alces americanus*)–habitat–climate relationships on Isle Royale illustrate the difficulties of attributing cause and effect even in very simple ecosystems ([Vucetich and Peterson 2004](#)). This case study stands out because researchers have explored multiple factors at the same time, have been excessively cautious in the language they use to attribute causality, and have constantly updated their views concerning the functioning of the ecosystem as new data becomes available. Shifting the research focus from ‘trophic cascades’ to ‘food webs’ in this way can help overcome the subtle yet troublesome overreliance on logical fallacies in studies of carnivores’ ecological roles ([Eisenberg et al. 2013](#)).

6. *Most of the ‘best evidence’ comes from ecosystems that do not represent the majority of the earth’s surface or species*

Although there are still some large tracts of relatively intact land in some places, the reality is that the majority of the earth’s surface has been substantially altered by humans, and continues to be altered, in a modern epoch now labelled as the Anthropocene ([Zalasiewicz et](#)

[al. 2008](#); [Kueffer and Kaiser-Bunbury 2013](#)). Modern, human-dominated ecosystems typically comprise mixed land-uses including urbanisation, forestry, mining, hunting, recreation, agriculture (crops and/or livestock production) or other areas fragmented by roads, railways and fences, and containing exotic plant and animal species and artificial water sources ([Linnell 2011](#); [Fleming et al. 2012](#); [Mech 2012](#)). Most tests of the MRH, TCH and BMTCH have occurred in relatively intact ecosystems with relatively minor human footprints, such as the National Parks of Canada and the United States ([Hebblewhite et al. 2005](#); [Ray et al. 2005](#); [Hayward and Somers 2009](#); [Eisenberg 2011](#); [Kuijper et al. In press](#)). Where studied, however, the strength and utility of carnivore effects on food webs in human-modified systems appear dissimilar to those in less modified ecosystems (e.g. [Elmhagen et al. 2010](#); [Muhly et al. 2013](#); [Meadows et al. 2017](#); [Morgan et al. 2017](#)).

For example, the recolonization of wolves in Sweden resulted in widespread behaviour change by humans in their moose (*Alces alces*) hunting practices that precluded, or at least reduced, the anticipated numerical effects of wolves on moose ([Wikenros et al. 2015](#)). “Because most of the world’s habitat that will be available for future colonization by large predators are likely to be strongly influenced by humans..., human response behaviour may constitute an important factor that ultimately may govern the impact of large predators on their prey and thus on potential trophic cascades” ([Wikenros et al. 2015](#); pg. 18). This point is further underscored by the situation in South Africa, where the introduction or removal of large carnivores has largely been driven by economic incentives ([Lindsey et al. 2007](#)), and the long term ecological effects have been overlooked. In Kenya, the indirect effect of carnivores on tree communities was mediated by ranching practices and the spatial distribution of cattle corrals ([Ford et al. 2014](#)). Comparative analyses of mammalian food webs in protected areas versus human-dominated areas of Canada concluded that ‘human influence on vegetation may strengthen bottom-up predominance and weaken top-down trophic cascades in ecosystems’ and that ‘human influences on ecosystems may usurp top-down and bottom-up effects’ ([Muhly et al. 2013](#)).

Theories about the effects of large carnivores on food webs, as developed in relatively pristine areas, may not be readily transferable or applicable to the human-modified landscapes that make up the majority of the Earth’s surface ([Haswell et al. 2017](#); [Morgan et al. 2017](#)). This is because the direct and indirect effects of humans on all trophic levels may simply overshadow any carnivore effects ([Muhly et al. 2013](#); [Darimont et al. 2015](#); [Clinchy](#)

[et al. 2016](#); [Kuijper et al. In press](#)). Carnivores are but one potential causal factor in a multicausal world ([Vucetich and Peterson 2004](#); [Peterson et al. 2014](#); [MacNulty et al. 2016](#); [Engeman et al. 2017](#)), and restoring large carnivores into these human-modified systems without removing the many other, more important causal factors influencing biodiversity loss is unlikely to succeed in reversing the situation ([Allen and Fleming 2012](#); [Fleming et al. 2012](#)). This is not to say that carnivore restoration efforts are unnecessary or should be avoided ([Chapron et al. 2014](#)), but that we should more carefully consider the anticipated benefits of these actions against the biophysical and anthropogenic factors that mediate the top-down effects of carnivores.

Implications for large carnivore science and management

The prevalence of these six aforementioned issues in the literature on large carnivores (Tables 1–3) underscores our contention that evidence for the MRH, TCH and BMTCH is undeniably weaker than is often claimed in journal articles or public discourse. Syntheses and literature reviews of large carnivores' ecological roles should identify these issues, but they usually do not, instead routinely failing to assess the internal validity of the original studies reviewed, as described by Bilotta et al. ([2014](#)). When the individual empirical studies that make-up the content of these reviews are judged against Platt's ([1964](#)) criteria for strong inference, Hone's ([2007](#)) deconstruction of experimental design capabilities, or Sutherland and colleagues' ([2013](#)) 20 tips for interpreting scientific claims, it is clear that even literature reviews (e.g. [Ritchie and Johnson 2009](#); [Estes et al. 2011](#); [Ripple et al. 2014b](#)) seldom offer reliable guidance on the state of the literature addressing the MRH, TCH and BMTCH. These remain intriguing hypotheses, but they are each inadequately tested and not yet demonstrated for almost all large carnivores and contexts.

We fear that the debates about the issues we raise here (Tables 1–3) are heading towards the type of science denialism that plague medicine or climate science (see [Diethelm and McKee 2009](#)). In a growing number of cases, strong evidence against MRH, TCH and BMTCH is denied while promoting these hypotheses using tactics common to science denial in other disciplines, such as selectivity, use of logical fallacies, disregard of experimental work, and deference to correlations (for examples, see [Letnic et al. 2011](#); [Ripple et al. 2011](#); [Beschta et al. 2014](#); [Forsyth et al. 2014](#); [Johnson et al. 2014](#); for responses, see [Hodges 2012](#); [Squires et al. 2012](#); [Fleming et al. 2013](#); [Allen et al. 2014a](#); [Winnie 2014](#); [Allen and West 2015](#)). Science denialism is often characterised by downplaying the scope of a threat ([Russell and](#)

[Blackburn 2017](#)). In the field of large carnivore science, this is clearly manifest in claims that carnivores are not a major problem for livestock producers or game ranchers (e.g. [Forsyth et al. 2014](#)). It is also manifest in claims that native large carnivores will suppress unwanted exotic species while denying that the same native carnivores can also suppress the threatened native species they are assumed to provide protection for (see [Fleming et al. 2013](#) or [Allen and Fleming 2012](#) for discussion). Dismissing or downplaying the legitimacy of scientific criticisms as mere ‘controversy’ or ‘debate’ (e.g. [Ritchie et al. 2014](#); [Newsome et al. 2015](#)) is also a form of passive science denialism. In truth, carnivores can have direct and indirect positive, negative or neutral impacts on social, economic and environmental values, and these impacts can change from time to time and place to place ([Chamberlain et al. 2014](#); [Haswell et al. 2017](#)). But emphasizing ‘the good’ while downplaying ‘the bad’ only produces ‘the ugly’ literature on carnivore science, while also fostering the rise of invasive species science denialism ([Russell and Blackburn 2017](#)). Such post-truth incredulities over evidence risks reversing progress in a field that is tackling some of the most important and engaging questions in modern ecology – namely, how does society restore and coexist with large fauna in human-occupied landscapes ([LaRue et al. 2012](#); [Chapron et al. 2014](#)) and what may be the ecological outcomes of this restoration effort?

Debates about the scientific understanding of, and appropriate management response to, large carnivore impacts are not new. For example, in Alaska and northern Canada there has been an ongoing debate about the impact of wolf and grizzly bear (*Ursus arctos*) predation on moose and caribou (*Rangifer tarandus*) populations for decades (e.g. [Orians et al. 1997](#); [Kennedy and Fiorino 2011](#)). The discourse has centred on the extent to which lethal control of wolf and bear populations will lead to an increase in the harvestable surplus of moose and caribou. An enormous amount of intensive research, of both descriptive and experimental types (reviewed by [Boertje et al. 2010](#)), has been conducted in the region since the 1970’s with the aim of understanding predator-prey relationships. But just like the Yellowstone region ([MacNulty et al. 2016](#)), there is still huge uncertainty and controversy about the nature of these trophic interactions and their consequences for management despite this considerable research investment (e.g. [Van Ballenberghe 2006](#); [Boertje et al. 2010](#); [Kennedy and Fiorino 2011](#)). Lessons that can be extracted from this ongoing saga include: (1) even with massive investment in research over many decades in relatively simple ecosystems it can still be a challenge to understand the nature of interactions between predators and prey, let alone the wider ecosystem impacts of human intervention on lower trophic levels; (2) valuable insights

can be obtained by exploring such relationships through the lens of predator-prey theory and demographic models, an approach which has been almost absent from the recent generation of trophic cascade studies (Tables 1–3); and (3) competing scientific results can rapidly be included into what are essentially value debates about different worldviews. The maturation of this controversy clearly shows how important it is to be aware of the intrinsic uncertainty and context-dependence (in time and space) of any research results, and of the need to clearly distinguish science from values in policy debates.

There are, of course, studies that are not encumbered by the six issues we raise, studies that do indeed provide strong support for the MRH, TCH and BMTCH. Much of this can be found in literature from marine, aquatic and invertebrate systems ([Heath et al. 2014](#); [Meadows et al. 2017](#)), or systems and models where bottom-up processes are relatively predictable, stable and controllable. Reliable work on MRH, TCH and BMTCH in terrestrial systems is only beginning to catch up to these disciplines. Literature reviews and syntheses are important as the field develops, but as described above, most of the reviews presently available are inadequate. There is, therefore, an urgent need for a systematic review (*sensu* [Pullin and Knight 2009](#)) of terrestrial studies that have used only manipulative experiments to investigate these hypotheses—experiments inclusive of paired treated and non-treated areas, sampled before and after treatments (e.g. carnivore removal or addition) over sufficient temporal and spatial scales to detect cascading responses of predators, prey and plants. A systematic review of such experimental studies, which excludes low-inference studies and summarises the results of only those with the actual capacity to assess causal processes, may produce useful insights into underlying ecological processes and be of great value to carnivore managers ([Pullin and Knight 2009](#); e.g. [Boertje et al. 2010](#)). It would also yield lessons on how to do more such research on different species, and in different contexts.

Many authors have called for such large-scale, long-term manipulative experiments investigating the removal or addition of large carnivores (e.g. [Glen et al. 2007](#); [Ritchie et al. 2012](#); [Newsome et al. 2015](#)). Although such experiments are expensive and difficult to achieve because of the logistical challenges arising from the massive scales that large carnivores utilise, they can and have been done in some places (e.g. [Eldridge et al. 2002](#); [Hayes et al. 2003](#); [Hebblewhite et al. 2005](#); [Allen et al. 2013a](#); [Marshall et al. 2013](#); [Allen et al. 2014b](#); [Christianson and Creel 2014](#); [Ford et al. 2014](#); [Hervieux et al. 2014](#); [Ford et al. 2015b](#); [Mitchell et al. 2015](#)). These have often, but not always, shown support for elements of

the MRH, TCH and BMTCH; less so for dingoes ([Allen et al. 2014b](#)) but more so for wolves ([Winnie and Creel 2017](#)). It is unlikely that many large carnivores will be subject to experimental studies like these, or like the famous Kluane project on the Canada lynx (*Lynx canadensis*) and snowshoe hare (*Lepus americanus*) system ([Krebs et al. 2001](#)). As a consequence, it is highly unlikely that we will ever have access to knowledge from such experiments for most large carnivores. Thus, a systematic review of studies testing the MRH, TCH and BMTCH with only strongly-inferential methods will be all the more valuable. It must also be remembered that while well-designed and implemented experiments will greatly advance our understanding of theoretical ecological principles ([Engeman et al. 2017](#)), the portability of their results may still be limited ([Schmitz et al. 2000](#); [Haswell et al. 2017](#); [Morgan et al. 2017](#)).

Our focus on improving research rigour is not intended to imply that observational or correlative ecological studies are not useful. Such studies are absolutely crucial to capture the broad spatial and temporal dynamics over which large carnivores and their prey interact ([Barley and Meeuwig 2016](#)). However, we argue that researchers need to exercise a greater degree of caution in the interpretation and communication of studies on the MRH, TCH and BMTCH, no matter how they are designed and conducted, and especially when they are used as the basis for radical changes in carnivore management and policy – including cases where lethal control and reintroduction are used. The associated biases, uncertainties, and ability to make inferences need to become ever more central parts of the communication of research results ([Johnson et al. 2015](#)). While we hope that scientists should manage this within the pages of peer-reviewed journals, additional challenges arise when trying to communicate uncertainty to the wider public ([Dixon and Clarke 2013](#)). In such contexts it is normally impossible to successfully communicate such intrinsic limitations, making it all the more important that authors take extreme care to not oversell the generality of their findings, nor allow others to do so, and clearly separate between scientific findings and the various normative policy or management action contexts within which these findings might be operationalised.

The reality is that the knowledge available to wildlife managers will at best be limited to a solid understanding of the natural history and ecology of the predators, their prey, and the ecosystem, and based largely on data derived from time series, cross-site comparisons, ‘natural experiments’ or other correlative studies ([Barley and Meeuwig 2016](#); [MacNulty et al.](#)

[2016](#)). A good understanding of species ecology can serve to exclude spurious or unreasonable interpretations of correlative data, and such studies can also exclude certain hypotheses or provide indirect support for other hypotheses for which experiments could be designed to provide a definitive test (e.g. [Platt 1964](#); [Kershaw 1969](#); [Underwood 1997](#); [Fairweather and Quinn 2006](#)). While these types of lower-inference studies may not overcome all the aforementioned issues we describe, they do have the advantage of being far cheaper and faster to conduct under a wide range of different ecological conditions, which can address problems associated with the transferability of knowledge between contexts. Ideally, conservation actions should be monitored within an adaptive management system that can be used to permit the study of system responses to specific management interventions ([Fleming et al. 2014](#); [Johnson et al. 2015](#)). This provides insights into how the system functions and how management actions produce outcomes. Certain forms of carefully designed adaptive management exercises can even be viewed as quasi-experiments ([Williams and Brown 2014](#); [Johnson et al. 2015](#)).

Given the perilous conservation situation of many large carnivore species, there is a clear need to act based on the best available knowledge at any given time ([Ripple et al. 2016a](#)). However, manipulative experiments clearly trump anecdotal, observational and/or correlative information for their informative value, and should therefore be valued more highly in the decision making process ([Platt 1964](#); [Fleming et al. 2013](#)). While the weight of evidence for the general role of large carnivores in triggering trophic cascades is indeterminate at this time (but we look forward to this potentially changing one day), we caution researchers and science communicators to carefully consider the implications of simultaneously advocating for both large carnivore conservation and the primacy of top-down trophic cascades. These two forms of advocacy need not be linked – carnivore conservation can often be justified on a number of moral, ethical, and existential grounds that have nothing to do with trophic cascades. At one extreme, such advocacy may contribute towards specious reintroduction efforts that divert funds from broader conservation goals and/or place the livelihoods of local people at risk ([Ford et al. 2017](#)). On the other extreme, we recognize that there will be no perfect study to ever ‘close the book’ on the prevalence of trophic cascades, regardless of their occurrence in nature. Because strongly-inferential, long-term, manipulative studies will be difficult to implement in a cost-effective and timely manner to support these decisions, we argue that knowledge of trophic cascades must be considered in management deliberations but should not necessarily determine their outcome.

Whether or not society should or shouldn't restore large carnivores is outside the scope of our present analysis (but see [Lewis et al. 2017](#)), and in the end, how large carnivores are managed is a judgement that society must make, and which will largely be based on which species (predator or prey or human interest) is given priority over another. In the Canadian case of Hervieux et al. ([2014](#)), for example, the immediate interests of ungulates were ultimately favoured over those of the wolves. Whereas, in the familiar Yellowstone story (e.g. [Middleton 2014](#)), the interests of wolves were ultimately favoured over those of the ungulates. Whether large carnivores are viewed as a 'good thing' or a 'bad thing' for an ecosystem largely rests on the attention given to which species (livestock, invasive pests, game species or threatened native fauna) carnivores happen to be killing at the time ([Allen et al. 2011b](#); [Mech 2012](#)). As carnivore conservationists ourselves, we relish any excuse to promote their conservation and recovery where it is needed and possible. But as scientists, we lament the lack of objectivity and critical thinking underpinning the current 'parental affection' (*sensu* [Chamberlin 1890](#)) towards the MRH, TCH, and BMTCH and the extent to which this affection is used to legitimise selected views on carnivore management.

Upon reflection, we also observe that debates about large carnivore management (Tables 1–3) are often not so much about differing beliefs or views about carnivores' actual functional roles, but more so about the quality of scientific evidence people are willing to accept. Large carnivore conservation is a bold and historically-novel judgement which must inevitably be made on incomplete ecological evidence. Ecological evidence alone is insufficient to make decisions, which must also account for the ethical, cultural and socio-political factors that shape decision making in society (e.g. [Van Ballenberghe 2006](#); [Mech 2010](#); [Trouwborst 2010](#); [Fleming et al. 2014](#); [Olson et al. 2015](#); [Trouwborst 2015](#); [Marshall et al. 2016](#); [Lewis et al. 2017](#)). We hope that the issues we raise here prompt deeper consideration of actual evidence, leading to an improvement in both the rigour and communication of large carnivore science, because the fates of many large carnivores and the integrity of associated ecological processes are depending on it.

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Tables

Table 1 – Some recent lines of debate discussing large carnivores' roles in trophic cascades in Australia, demonstrating that evidence for the ecological roles of dingoes is equivocal, primarily due to the six issues described in the present article.

Debated topic	Chronological order	Reference
Trophic cascades following dingo control	1	Wallach and O'Neill 2009
	2	Allen 2010
Ecological niche of dingoes	1	Fleming <i>et al.</i> 2012
	2	Johnson and Ritchie 2013
	3	Fleming <i>et al.</i> 2013
	4	Claridge 2013
Dingo predation risk to fauna	1	Dickman <i>et al.</i> 2009
	2	Allen and Fleming 2012
Methodological problems with dingo studies	1	Allen <i>et al.</i> 2011a
	2	Letnic <i>et al.</i> 2011
	3	Allen <i>et al.</i> 2011b
	4	Glen 2012
	5	Allen <i>et al.</i> 2013b
Cause of historical declines of marsupials	1	Johnson <i>et al.</i> 2007
	2	Allen 2011
Importance of dingo social structure	1	Wallach <i>et al.</i> 2009
	2	Allen 2012b
Trophic cascades following dingo control	1	Colman <i>et al.</i> 2014
	2	Allen 2015b
	3	Colman <i>et al.</i> 2015
Effects of dingoes on sheep	1	East and Foreman 2011
	2	Allen and West 2013
	3	Forsyth <i>et al.</i> 2014
	4	Allen and West 2015
Trophic cascades following dingo control	1	Allen <i>et al.</i> 2013a
	2	Johnson <i>et al.</i> 2014
	3	Allen <i>et al.</i> 2014a
	4	Allen <i>et al.</i> 2014b
	5	Hayward and Marlow 2014
	6	Nimmo <i>et al.</i> 2015
	7	Hayward <i>et al.</i> 2015

Table 2 – Some recent lines of debate discussing large carnivores’ roles in trophic cascades in North America, demonstrating that evidence for the ecological roles of wolves is equivocal, primarily due to the six issues described in the present article.

Debated topic	Chronological order	Reference
Wolf-induced behaviourally-mediated trophic cascades in Yellowstone	1	Ripple and Beschta 2004 ¹³⁸³
	2	Kauffman <i>et al.</i> 2007
	3	Ripple and Beschta 2007 ¹³⁸⁴
	4	Kauffman <i>et al.</i> 2010
	5	Kimble <i>et al.</i> 2011
	6	Winnie 2012
	7	Beschta and Ripple 2013
	8	Kauffman <i>et al.</i> 2013
	9	Middleton <i>et al.</i> 2013a
	10	Beschta <i>et al.</i> 2014
	11	Winnie 2014
	12	Painter <i>et al.</i> 2015
Willow recovery in Yellowstone following wolf reintroduction	1	Ripple and Beschta 2003
	2	Despain 2005
	3	Ripple and Beschta 2006
	4	Wolf <i>et al.</i> 2007
	5	Beyer <i>et al.</i> 2007
	6	Bilyeu <i>et al.</i> 2008
	7	Creel and Christianson 2009
	8	Tercek <i>et al.</i> 2010
	9	Johnston <i>et al.</i> 2011
	10	Middleton <i>et al.</i> 2013a
	11	Marshall <i>et al.</i> 2013
	12	Marshall <i>et al.</i> 2014
	13	Smith <i>et al.</i> 2016
Trophic cascades and Mexican wolves	1	Beschta and Ripple 2010
	2	Mech 2012
Wolf effects on lynx	1	Ripple <i>et al.</i> 2011
	2	Hodges 2012
	3	Squires <i>et al.</i> 2012
	4	Wirsing <i>et al.</i> 2012
Wolf effects on bears	1	Ripple <i>et al.</i> 2014a
	2	Barber-Meyer 2015
	3	Ripple <i>et al.</i> 2015
Ethics and effects of predator control for moose conservation in Alaska	1	WMRC 1996
	2	Orians <i>et al.</i> 1997
	3	Van Ballenberghe 2006
	4	Boertje <i>et al.</i> 2010
	5	Kennedy and Fiorino 2011

Table 3 – Some recent lines of debate discussing large carnivores’ roles in trophic cascades in Europe, demonstrating that evidence for the ecological roles of large carnivores is equivocal, primarily due to the six issues described in the present article.

Debated topic	Chronological order	Reference
Human influence on trophic cascades in Europe	1	Melis <i>et al.</i> 2009
	2	Kuijper 2011
	3	Dorresteijn <i>et al.</i> 2015
	4	Kuijper <i>et al.</i> 2016
	5	Ritchie <i>et al.</i> 2016
Large carnivore impacts on mesocarnivores	1	Palomares <i>et al.</i> 1995
	2	Palomares <i>et al.</i> 1998
	3	Sunde <i>et al.</i> 1999
	4	Linnell and Strand 2002
	5	Helldin <i>et al.</i> 2006
	6	Elmhagen and Rushton 2007
	7	Kowalczyk <i>et al.</i> 2009
	8	Pasanen-Mortensen <i>et al.</i> 2013
	9	Wikenros <i>et al.</i> 2014
	10	Pasanen-Mortensen and Elmhagen 2015